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STUDIES ON THE OPHIOGLOSSACEÆ

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THE family of the Ophioglossaceæ comprises the three genera—Ophioglossum, Botrychium and Helminthostachys, which are all evidently related, but whose affinities with the other Pteridophytes are not so clear, and there is a good deal of difference of opinion as to where they should be placed. Most botanists agree that the Ophioglossaceæ are related to the true ferns, but this view is not universally accepted, although the results of the more recent investigations tend to strengthen this conclusion.

The most marked feature of the family is the peculiar fertile leaf segment or spike; and the present paper is mainly concerned with the question of the morphologic nature of this sporophyll.

During the past year the writer had an opportunity of collecting a large amount of material of the Ophioglossaceæ in Ceylon, Singapore and Java. This included several species of Ophioglossum, one of Botrychium, and the monotypic Helminthostachys,— so that it has been possible to make a first-hand study of all the genera belonging to the family. The following account of the morphology of the leaf is based mainly upon a study of this material.

THE MORPHOLOGY OF THE SPOROPHYLL.

In all of the Ophioglossaceæ the sporophyll consists of a fertile and a sterile segment. The former (Figs. 1, 3, 4, 6, 7) is a stalked structure, the peduncle being often very long. The sporangia are in two rows in Ophioglossum, but in the other genera the fertile portion of the spike is more or less extensively branched,

this being very marked in the larger species of Botrychium. The two segments of the sporophyll may be almost entirely separate, *e. g.*, *Ophioglossum bergianum*, *Botrychium ternatum*, or the fertile segment may be apparently an outgrowth of the base of the sterile segment or from above its base.

The earlier views of the morphologic value of the fertile leaf segment were strongly influenced by the prevailing theory that the fertile portion was a secondary development of originally sterile leaf tissue, and therefore must be homologized with some portion of the sterile leaf. The belief more generally current at present that the fertile structures of the sporophyll are older than the sterile ones, inclines toward a different interpretation of the real nature of the fertile segment.

Bower (Studies in the Morphology of Spore-producing Members, II, Ophioglossaceæ. London, 1896) has given a very complete account of the different theories that have been advanced to explain the morphology of the fertile spike in the Ophioglossaceæ, and we shall merely give here a brief summary of the more important of these. Mettenius (Farne des Bot. Garten zu Leipzig. 1856, p. 119) regarded the two parts of the leaf as of equal importance, but gives no data as to their method of origin,—whether by the equal branching of a common primordium or otherwise. Later writers, *e. g.*, Holle (Bot. Zeit. 1875, p. 271) and Goebel (Schenk's Handbuch, vol. 3, p. 111) consider the fertile spike as the equivalent of the fertile pinnæ of such a fern as Aneimia. The former considers the single median spike to be the result of the coalescence of two lateral pinnæ; the latter as a single pinna which arises in a median position.

Bower himself has made the most complete study of the development of the spore-bearing parts of the Ophioglossaceæ that has ever been made. He concludes that the spike of Ophioglossum is morphologically equivalent to the single sporangium of Lycopodium. In this view he has the support of Strasburger (Bot. Zeit., 1873) and Celakovsky (Pringsheim's Jahrb., 1884, vol. **14**). Bower has, however, more recently described a most remarkable species of Ophioglossum (Ann. of Bot. **18**, p. 205, 1904) *O. simplex* Ridley, which makes possible another interpretation of the nature of the spike, *i. e.*, that it is a terminal and not a lateral organ. The writer (Mosses & Ferns, 2d edit., p. 600) in view of the dis-

covery of this remarkable form, has ventured the hypothesis that in *O. pendulum* the sporangiophore may also be terminal. In order to make a thorough investigation of the question, the collections of material already referred to were made and the results of this study and the conclusions to be drawn from it are given in the present paper.

THE GENERAL MORPHOLOGY OF THE SPOROPHYLL.

Ophioglossum.

The genus Ophioglossum comprises, according to Bitter (Engle & Prantl, Die Naturlichen Pflanzenfamilien, 1 Theil. Abt. 4, p. 466) about thirty species, but it is probable that the number is much greater, as the species have not been critically studied in some regions where the genus is well represented. Bitter recognizes three sections of the genus, Euophioglossum Prantl, including most of the terrestrial species; Ophioderma Presl, with *O. pendulum* L. and *O. intermedium* Hooker; and Cheiroglossa Presl. with the single species, *O. palmatum*. The subgenus, Rhizoglossum Presl, is also sometimes recognized to include the single species *O. bergianum*.

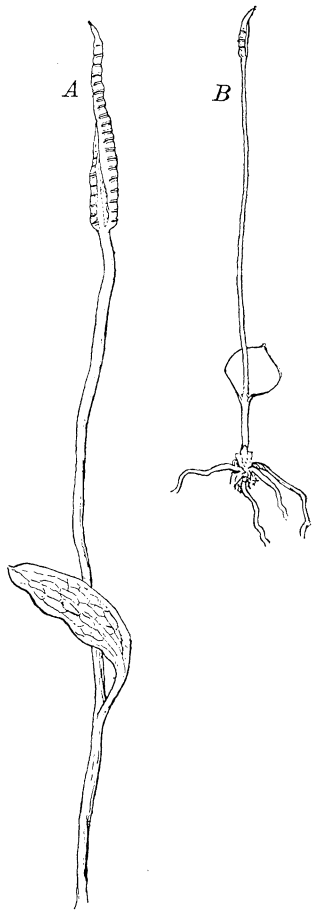

Fig. 1.— *A*, Sporophyll of *Ophioglossum moluccanum* Schlecht. natural size; *B*, Small form of *O. moluccanum* (?) natural size.

The great majority of the species belong to the first section, Euophioglossum. The writer collected a number of species in Ceylon and Java, but it was found very difficult to identify them, as in neither the collections at Peradeniya nor Buitenzorg was the genus well represented, and there is evidently very much confusion as to the species.

Raciborski, who has published a list of Javanese Pteridophytes (Die Pteridophyten der Flora von Buitenzorg, Leiden, 1898) gives only one terrestrial species, *O. moluccanum* Schlecht.; but it is evident from the writer's collections that there are at least four species belonging to Euophioglossum in western Java and possibly more.

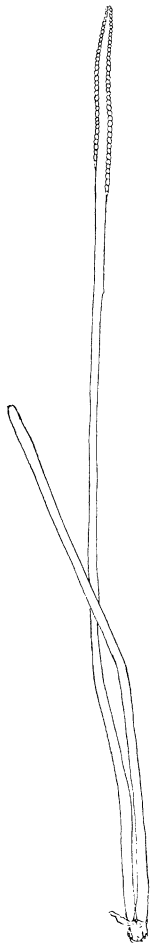

FIG. 2. — Plant of *Ophioglossum simplex* Ridley × ⅔ (after Bower).

What seems to be the typical *O. moluccanum* (fig. 1, A) is a species of moderate size. The specimen shown has a sterile leaf somewhat smaller than usual, but otherwise is typical. One of the smaller forms of the same (?) species is shown in fig. 1, B. In both of these the sterile lamina is small, while the peduncle of the spike is very long and not very much inferior in thickness to petiole below the junction of the spike and the sterile lamina. Most of the other species of the section, *e. g.*, *O. vulgatum* L., *O. californicum* Prantl, *O. reticulatum* L., etc., agree in the main with *O. moluccanum*, and in none of these is there anything in the external morphology of the adult sporophyll to forbid the assumption that the sterile lamina is a lateral appendage of the spike.

The second section of the genus, Ophioderma, comprises *O. pendulum* L., *O. intermedium* Hook. and probably also *O. simplex* Ridley. In the latter species (fig. 2), which was discovered by Ridley in Sumatra, the fertile leaf consists of a narrow basal part without any lamina, terminated by a spike similar to that in *O. pendulum*, and it was assumed to be the nearest relative of this species. There is, however, no peduncle developed as is the case in *O. pendulum* and *O. intermedium*. It is well known that in *O. pendulum* (see Fig. 3) the short peduncle of the spike which apparently arises from the lamina itself, is continued into a sort of thickened mid-rib which is not developed above the insertion of the peduncle

of the spike, and the latter may very well be interpreted as the apex of the leaf, the lamina being lateral and closely coherent with its basal portion.

In all the species of Ophioglossum the growth of the basal part of the young sporophyll is very much more active than that of the lamina which remains relatively small, although the young spike is conspicuous in the early stages. This is especially marked in *O.*

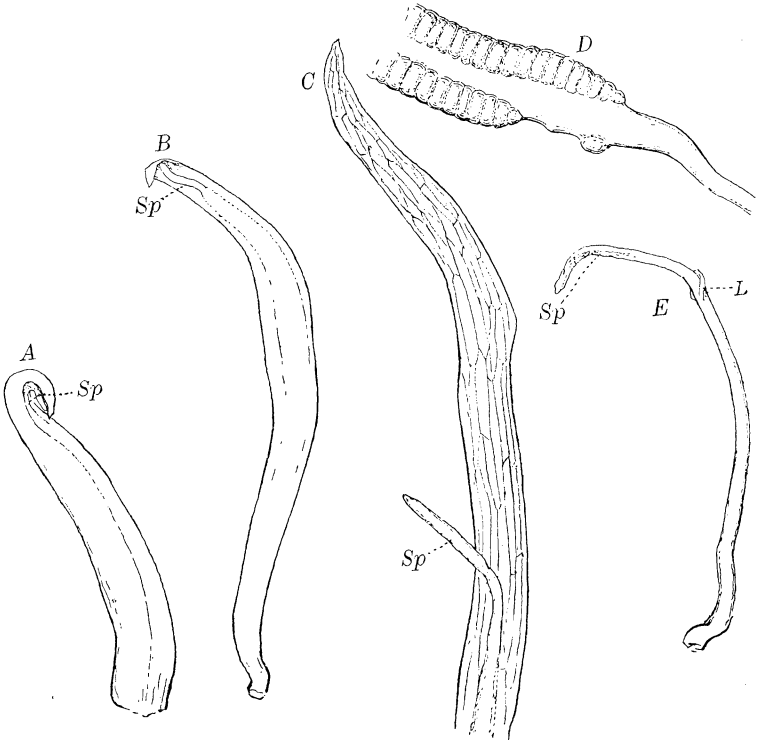

FIG. 3.— *A*, Young sporophyll of *Ophioglossum* (*Ophioderma*) *pendulum* L.. × 2; *B*, an older stage, natural size; *C*, a still older stage; *D*, base of a large spike, natural size; *E*, a small sporophyll in which the sterile lamina, *L*, is very greatly reduced, natural size.

pendulum (Fig. 3). This is the largest of the genus, and is a striking epiphyte of the moist tropics of the old world, extending, however, to the Hawaiian Islands. The specimens figured were collected in the botanical garden at Singapore.

In the youngest specimen shown (Fig. 3, A), the thick fleshy

leaf base terminates in a very small pointed lamina that is usually bent over, suggesting the circinate vernation of the true ferns. In most of the terrestrial species of Ophioglossum the young leaf is folded straight in the bud. Under the arched hood formed by the lamina is the young spike (*Sp.*) which almost equals the lamina in length.

Fig. 3, B, shows a somewhat older stage. The leaf has now become somewhat flattened, but there is no clear demarkation between the petiole and the small lamina. The fertile segment, which shows as yet no differentiation of the peduncle and spike, is conspicuous, and merges gradually into the thick petiole of the leaf whose margins are more or less distinctly winged and pass imperceptibly into the lamina above the insertion of the fertile segment. The interpretation of the latter as terminal and the sterile portion as a lateral appendage coherent with it would seem entirely plausible. An interesting case is shown in Fig. 3, E, where the lamina is almost entirely suppressed, and the terminal character of the spike is very evident.

As the leaf develops there is a very great increase in size of the lamina, which, in some of the largest individuals collected in Ceylon and Java, reached a length of one and one-half metres, or even more. These large leaves usually have the lamina dichotomously divided, and strikingly resemble the long drooping leaves of some species of Platycerium. Nevertheless even in these larger leaves the segments are quite destitute of a mid-rib. This stops at the base of the peduncle of the spike into which it is continued. The spike in these large specimens is correspondingly large, and sometimes attains a length of 25 to 30 centimetres, with a breadth of more than a centimeter (Fig. 3, D).

Undoubtedly allied to *O. pendulum* is the rare *O. intermedium* Hook. (Fig. 4). This is also perhaps the nearest ally of *O. simplex*. In the ordinary form (Fig. 4, A, B) this is not unlike a small specimen of *O. pendulum*, but it is rigidly upright instead of lax and drooping, the peduncle is longer and the lamina of the leaf much smaller and more sharply separated from the petiole. As in *O. pendulum*, however, the petiole is prolonged into the peduncle of the spike with the same mid-rib like thickening, caused by the coherence of the basal part of the peduncle with the lamina.

Even in the small number of specimens collected (the plant is an extremely rare one) a number of very interesting variations were found, some of which approximated quite closely the condition found in *O. simplex*. In these the lamina was greatly reduced, and in one case (Fig. 4, E) formed merely the narrow wing along the margin of the petiole and peduncle of the spike. In the other

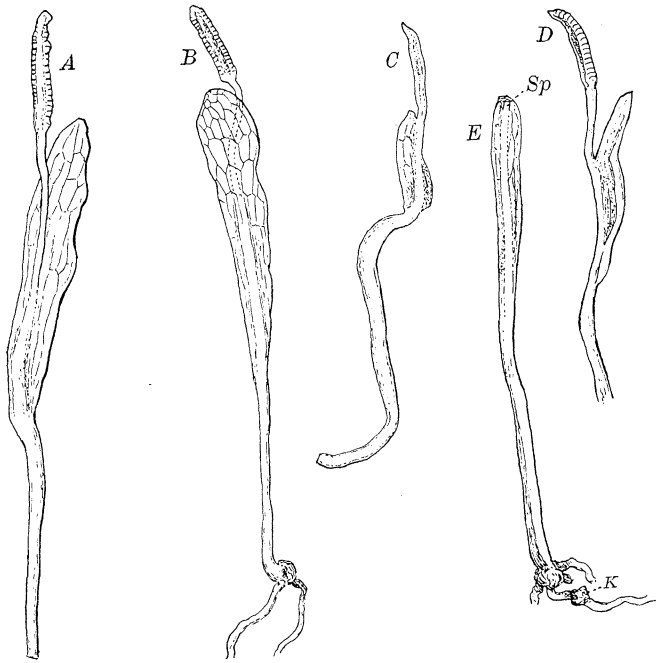

FIG. 4.— *Ophioglossum* (*Ophioderma*) *intermedium* Hook. several plants reduced about ½, showing variation in form; *K*, root-bud.

cases the lamina was wider and its apex free, but even in these the lamina was very small, and the terminal position of the spike extremely evident (C, D).

In both *O. pendulum* and *O. intermedium* the spike is more flattened than in the section Euophioglossum, and the central sterile portion wider in proportion. Stomata are almost entirely absent from the spike of *O. pendulum*, and the few that are occasionally found are confined to the central part. In *O. intermedium* the stomata are more numerous than in *O. pendulum*, but much less numerous than in *O. moluccanum*, for example, where they also occur upon the epidermis of the wall of the sporangium.

The third section, Cheiroglossa, represented by the monotypic *O. palmatum* L. of the American tropics differs from the others of the genus in having, usually, several spikes which are not generally borne in the median plane of the leaf, but are inserted near the margin. Bower (loc. cit., figs. 116–117) has shown that there may occasionally be a single spike which is then borne in the same position as in *O. pendulum*. He supposes that *O. palmatum* has been derived from the form with a single median spike like that of *O. pendulum* by branching of the spike, which not infrequently occurs in the latter species as well as in some others. The separation of the originally connected spikes he assumes has been the result of the great expansion of the lamina, which is much broader in *O. palmatum* than in any other species. Unfortunately the developmental history of the sporophyll in *O. palmatum* is quite unknown.

THE YOUNG SPOROPHYLL.

The differentiation of the two parts of the sporophyll takes

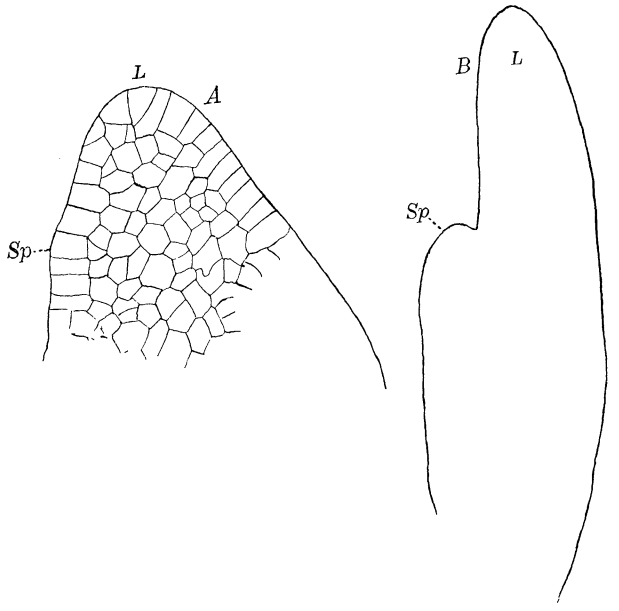

FIG. 5.— *A*, Nearly median section of a very young sporophyll of *O. pendulum*, × about 90; *B*, section of an older sporophyll, × 50; *Sp.* the apex of the spike; *L*, the sterile leaf-segment.

place at a very early period, and at this time the fertile spike is already evident as a conspicuous protuberance on the adaxial side of the leaf rudiment not far from its apex. Both divisions of the young sporophyll terminate in an apical cell, and both apparently grow in the same way.

Fig. 5, A, shows a nearly median section of a very young sporophyll of *O. pendulum*. This is a broadly conical body upon whose inner (adaxial) face there is a slight prominence (*Sp.*) the apex of the young spike. Fig. 5, B, shows an older, but still very early stage, in which it is evident that the spike rudiment extends completely to the base of the young leaf, with which it is adherent except at the extreme tip. The apex of the young spike is directed upward and its axis is almost parallel with that of the sterile leaf segment. From Bower's figures of corresponding stages in *O. vulgatum* it is clear that a very similar condition of things prevails in that species. In such a stage as that shown in Fig 5, B, the relation of the fertile and sterile segments is not unlike that of a stem apex and leaf, and the condition of things here present would very well lend itself to the interpretation of a terminal spike with a subtending sterile lamina. At this stage the vascular bundles are not yet differentiated, and the arrangement of these in the young leaf still remains to be made out.

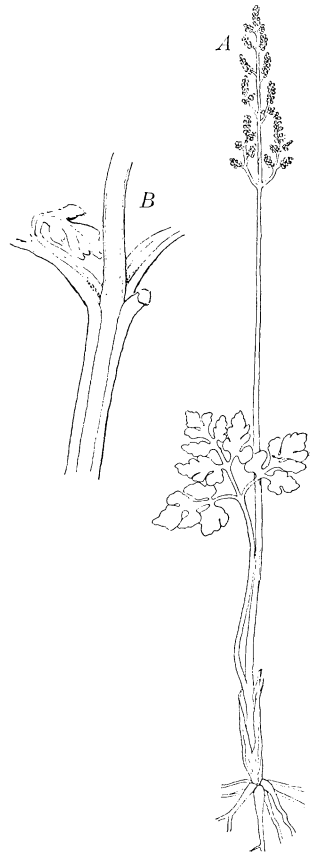

Fig. 6.— *A*, Plant of *Botrychium ternatum* Sw., × ½; (after Luerssen); *B*, base of the spike in *B. lanuginosum* Wall., slightly enlarged.

Botrychium.

In the second genus, Botrychium, most of whose species are plants of the temperate zones, both the fertile and sterile segments of the leaf as is well known, except in some

simple forms of *B. simplex,* are more or less extensively branched. This is especially marked in such large species as *B. virginianum* and *B. lanuginosum.*

The relation of the fertile and sterile periods is essentially the same as in Ophioglossum, and there is the same variation in the point of divergence of the two leaf segments. Thus in *O. obliquum* Muhl. the two are separated almost to the base. In *O. virginianum* and *O. lanuginosum* (Fig. 6, B) the spike appears to arise close to the lamina of the leaf or even above its base. No material was available for a critical study of this point in *B. virginianum,* but in *O. lanuginosum* Wall. where (see Engler & Prantl, loc. cit., p. 471) it is stated that the spike arises from the base of the sterile segment; even a casual examination will show that this is more apparent than real (see Fig. 6, B). If the leaf be looked at from in front it is very evident that the peduncle can be traced for a long distance below the bases of the sterile leaf segments, although only the anterior face is free, the inner face and sides being completely adherent to the base of the sterile segments.

HELMINTHOSTACHYS.

A similar condition to that found in *Botrychium lanuginosum* prevails in the third genus, Helminthostachys (Fig. 7), a monotypic genus of the Indo-Malayan region. This is much nearer to Botrychium, in its general morphology, than it is to Ophioglossum, although, in the character of both the prothallium and fertile spike, it is to some extent intermediate in character between the two genera.

In Helminthostachys the sterile segment, as in most species of Botrychium, is ternately divided, and the anterior margins of the stalks of the two lateral leaf segments are continued as more or less conspicuous wings enclosing the adherent base of the peduncle.

DISTRIBUTION OF THE VASCULAR BUNDLES.

A careful study of distribution of the vascular bundles of the leaf was made in most of the species that were available, to see

how far this harmonized with the theory of the terminal nature of the fertile spike. The arrangement of the bundles has already

FIG. 7.— *A*, Sporophyll of a small specimen of *Helminthostachys zeylanica* Hook., × ½; *B*, base of the spike, natural size.

been studied in the commoner European species, *O. vulgatum*, *O. lusitanicum* and *B. lunaria*. Bower has also investigated this in *O. bergianum*, and more recently in *O. simplex*, *O. pendulum* and *O. palmatum* (loc. cit. 1904). Of these forms the writer has examined *O. pendulum*, and in addition to this a number of other species which have not been hitherto studied.

In all of the species belonging to the section Euophioglossum that have been examined, there is given off from the vascular system of the rhizome a single leaf trace which divides at the base of the leaf into two strands. This is probably the case also in all the forms associated with *O. moluccanum* (see Fig. 8). According to Prantl, in *O. lusitanicum* each of these two bundles gives off a branch toward the adaxial side of the petiole which unite and

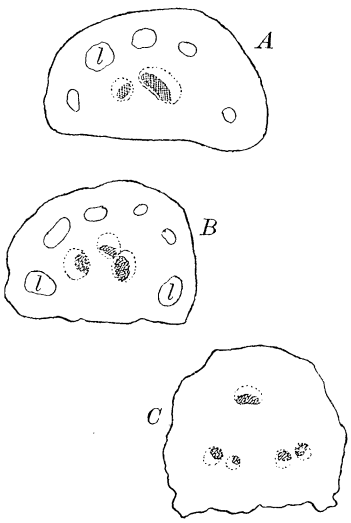

Fig. 8.—Three cross-sections of the lower part of the petiole of *Ophioglossum sp.*, × 25; *A*, *B*, at the base; *C*, higher up.

pass into the spike, the main trunks passing upward into the lamina. In the specimen shown in Fig. 8, which probably was not the typical *O. moluccanum*, while the leaf trace divides into two branches, as in *O. lusitanicum*, only one of these divided at the base of the leaf, so that at a point some distance above the base there are only three bundles, two of which are destined for the spike. The single bundle which is to supply the lamina is the result of the division of one of the two primary strands, the other half of which forms one of the adaxial bundles belonging to the spike.

O. MOLUCCANUM SCHLECHT.

A transverse section of the petiole in the typical *O. moluccanum*, made some distance below the point of separation of the two parts of the sporophyll (Fig. 9, A), shows four nearly equal vascular bundles, of which one is on the outer (abaxial) side, the other three on the adaxial side. As in all other species of Euophioglossum, these bundles are markedly collateral in structure. It is probable that the central adaxial bundle is due to the branching of one of the two adaxial bundles found near the base of the petiole.

If a section be made just below the point where the two parts of the leaf separate (Fig. 9, B), the three adaxial bundles are still recognizable, but the abaxial one has divided into several, which are evidently destined to supply the sterile leaf segment. A section taken a little higher up (C) shows plainly the bases of the two parts of the leaf. In the adaxial part, the peduncle of the spike, the original three adaxial bundles, are clearly evident, while in the lamina may be seen an increased number of bundles due to

the further ramifications of the abaxial bundles to form the reticulum of veins in the leaf segment. It is clear that in this species three of the four bundles of the petiole are continued unbroken into the spike, while only one of these contributes to the sterile leaf segment. This would certainly tend to confirm the view that the spike is the principal part of the leaf, and the lamina is secondary.

The base of the spike (Fig. 9, C, D) shows the three bundles, but above the base (E) these bundles may branch, so that a section higher up shows five bundles. The ramifications of the veins of the fertile part of the spike were not studied in detail.

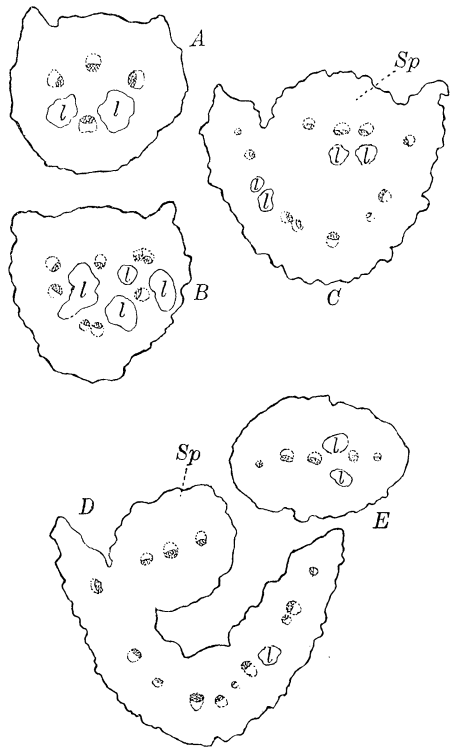

FIG. 9.— Five sections of the sporophyll of *O. moluccanum*; *A*, the petiole; *B*, *C*, intermediate; *E*, the peduncle of the spike; *l*, lacunæ; × 20.

OPHIOGLOSSUM SP.

Fig. 10 shows sections of a second form of Ophioglossum, collected at Buitenzorg, evidently specifically distinct from *O. moluccanum*. It was a plant of about the same size, but it differed both in the cordate sterile leaf and in the size and other characters of the spores. It is probable that Fig. 8, which shows the extreme lower part of the petiole, also belongs to this species. The lower part of the petiole in cross section shows but three bundles instead of four, the middle adaxial bundle being absent. In a section taken near the junction of the spike and lamina there were four abaxial bundles and five adaxial ones. It is not exactly clear as to the relation of the latter to the ramification of the two pri-

mary adaxial bundles, whose identity is not so clearly maintained as in *O. moluccanum*. In a section at the base of the lamina the

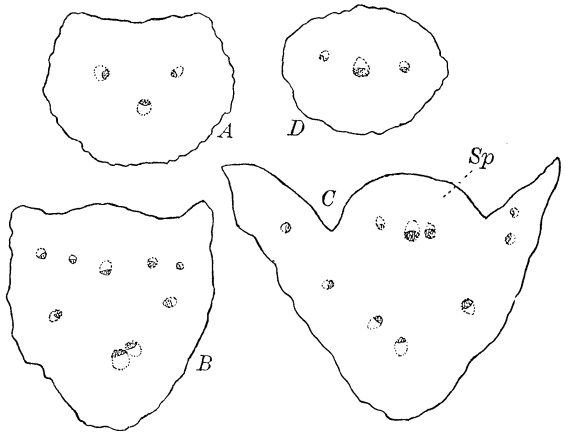

FIG. 10.— Four sections at different heights of the sphorophyll of *Ophioglossum sp.*; *A*, petiole; *B*, *C*, intermediate; *D*, peduncle; × 20.

arrangement of the bundles is very much the same as in *O. moluccanum*, and the three bundles of the spike are very similar. The triple arrangement continues into the spike, and a section made well above the base shows practically the same appearance.

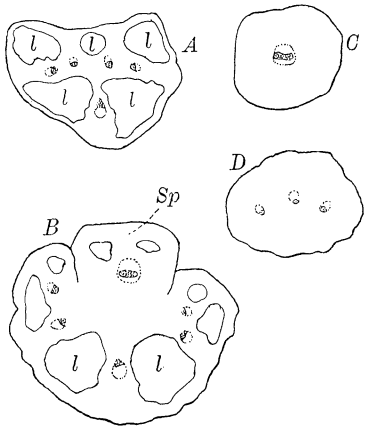

FIG. 11.—*Ophioglossum californicum* Prantl.; *A–C*, three sections of the sporophyll of a medium sized specimen; *D*, section of the peduncle from a larger specimen; × 20.

O. CALIFORNICUM PRANTL.

O. californicum is a small species from southern California. In the anatomy of the leaf it seems to follow pretty closely the description given by Prantl for *O. lusitanicum*. A section of the petiole (Fig. 11, A) shows four adaxial bundles, and a single abaxial one. If the section be made through the base of the peduncle and lamina (Fig. 11, B) the spike shows in some cases but a single large bundle, evidently formed by the coalescence of the adaxial bundles. There are five

bundles belonging to the lamina, of which the posterior one is apparently the original abaxial bundle, while the others are derived from the two outer of the four adaxial bundles. A large specimen which was examined showed three bundles in a transverse section of the peduncle (Fig. 11, D).

Ophioderma.

Bower has shown that in *O. pendulum*, *O. simplex* and *O. palmatum* there is not a single leaf trace, but the individual strands of the petiole join the vascular system of the rhizome directly. He also showed that the adaxial bundles which supply the spike in the fertile leaf of *O. pendulum* are quite absent from the petiole of the sterile leaf, which in section shows no bundles at all on the adaxial side. In the section Ophioderma the upper part only of the peduncle is free, the lower portion, as we have seen, being adherent to the lamina and merging insensibly into the common petiole of the sporophyll. Fig. 12 shows four sections at different heights from a leaf of *O. intermedium*. Near the base of the petiole there are five vascular bundles, of which the two on the adaxial side are noticeably larger than the three abaxial bundles. Somewhat higher up there are four adaxial bundles, evidently the result of a bifurcation of the two which are seen lower down. The three abaxial bundles remain unchanged except that they are somewhat further apart, corresponding to the broadening of the petiole at this point. Still higher up, where the base of the peduncle is coherent with the lamina, the former may be seen projecting somewhat from the leaf and containing three bundles, and the same number occurs in the free portion of the peduncle (Fig. 12, C & D).

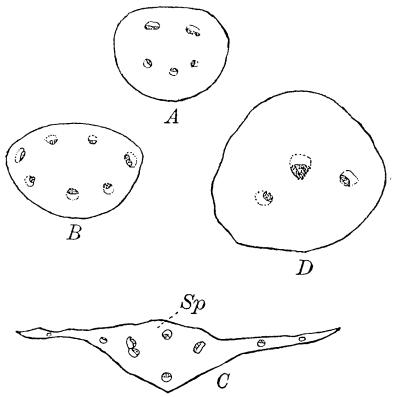

Fig. 12.— *Ophioglossum intermedium*; *A–C*, three sections of the petiole and lower part of lamina, × 6; *D*, section of free part of peduncle, × 20.

The very much larger leaves of *O. pendulum* show a correspondingly larger number of vascular strands. Fig. 13, A to D, shows sections through the petiole, base of lamina, and spike of a medium size specimen. In the former eighteen bundles could be seen, of which probably seven or eight are destined to supply the spike. In the basal part of the lamina six or seven adaxial bundles are plainly visible below the slightly projecting region which marks the coherent portion of the peduncle. In both this species and *O. intermedium* the free portion of the peduncle is comparatively slender, and the number of bundles less than in the broader basal part. In the specimen figured there were three bundles, of which the middle one was evidently doubled, and was clearly formed by the coalescence of some of the bundles before they left the adherent part of the peduncle. Higher up there were five bundles arranged in a semicircle. The same arrangement was found in the peduncle of a larger specimen (Fig. 13, E) taken from the spike which is shown in Fig. 3, D.

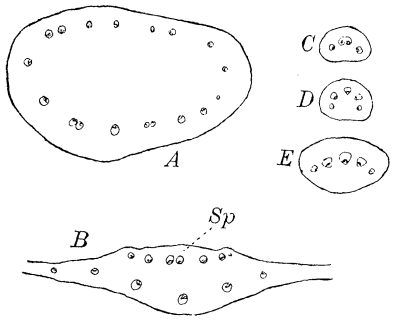

FIG. 13.— *Ophioglossum pendulum*; *A*, section of the petiole of the sporophyll; *B*, section of the base of the lamina and coherent peduncle, *Sp*; *C*, *D*, two sections of the free portion of the peduncle; *E*, section of the peduncle from a larger specimen; all figures × 4.

The complete absence of the adaxial strands in the petiole of the sterile leaf, even at its base, is a strong confirmation of the view suggested by both the older leaf and the younger stages that the peduncle really extends to the extreme base of the petiole and is joined directly to the rhizome.

BOTRYCHIUM.

The only species of Botrychium available for study was *O. lanuginosum* Wall. collected at Horton Plains in the uplands of Ceylon. The arrangement of the bundles in the leaf of this species agrees in the main with that of the other species that have been studied (see Bitter, loc. cit., p. 458). The leaf trace divides into

two at the base of the petiole, and these branches divide again somewhat higher up (Figs. 14, A to C). Of the four bundles thus formed, the two larger adaxial ones are those which supply the spike, the smaller abaxial ones supplying the lamina. In larger

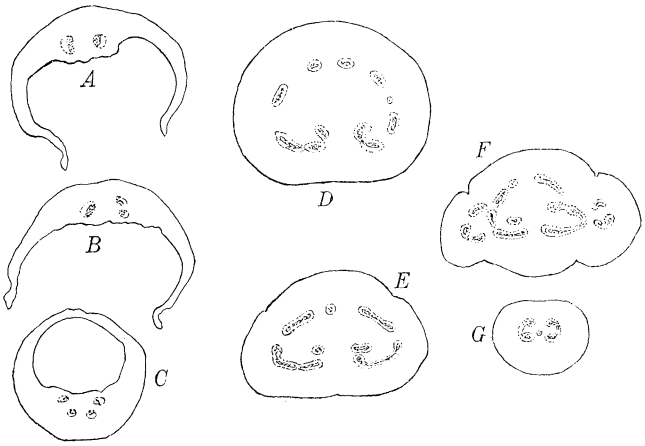

FIG. 14.— *Botrychium lanuginosum*; *A*, *B*, *C*, Sections through the base of the petiole; in *C*, the position is reversed from that of the others; *D–G*, sections of the petiole and upper part of the sporophyll of another specimen; × 4.

specimens of this species (Fig. 14, D), and the same is true in *B. virginianum*, there may be a subsequent branching of some of the bundles, so that a cross section of a stout petiole shows a larger number of bundles, sometimes as many as ten.

Sections made at the junction of the spike and lamina (Fig. 14, E) show anastomoses of some of the bundles which appear elongated in section, but there seems to be no regular rule governing the fusion of these. It is not quite clear whether any branches are given off from the spike bundles into the lamina, but this is probably the case in regard to the two lateral segments of the lamina. Within the peduncle of the spike in the larger specimens (Fig. 11, G) the two original bundles are again clearly defined, but in some of the smaller specimens these may be completely united into a single central bundle.

HELMINTHOSTACHYS.

Farmer & Freeman (On the Structure and Affinities of Helminthostachys zeylanica, Ann. of Bot. **17**, p. 421, 1899) state that in Helminthostachys there is, as in Euophioglossum and Botrychium, a single leaf trace which afterwards divides into several, usually seven or eight, within the petiole. As we have already seen, although the spike in Helminthostachys arises apparently from the base of the lamina, in reality its origin is lower down, and it may be traced for a long distance below the insertion of the sterile segments.

In a section made near the base of the petiole, it appears almost circular in outline with a ring of separate bundles. On the adaxial side, however, there are two other bundles within the outer circle. The number of bundles in the larger specimens collected by the writer was decidedly greater than that given by Farmer & Freeman (see Fig. 15, A). Higher up the section is no longer round, but slightly lobed, indicating the bases of the three branches of the ternately divided lamina, and on the adaxial side can be plainly seen a fourth lobe, which marks the position of the spike. This is bounded by two more or less conspicuous bodies, the sections of the wings that extend down the petiole from the lateral leaf lobes (Fig. 15, B & C). In this region the separate bundles of the basal part of the petiole are more or less coalescent, but the two adaxial bundles remain separate and are those which later extend into the spike. Still higher up the spike becomes more evident, and the two bundles belonging to it still more clearly separated. In the free portion of the peduncle the two crescent shaped bundle

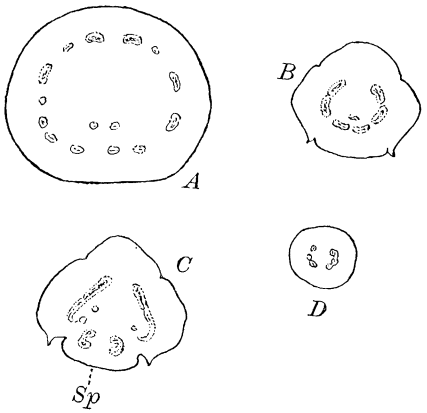

FIG. 15.— *Helminthostachys zeylanica*; *A*, section of the petiole of a large specimen, near the base; *B*, *C*, sections higher up, of the petiole of a smaller specimen; *D*, section of the peduncle; × 15.

sections are seen (Fig. 15, D), but it is evident that they are really composed of several coalescent bundles. A slight indication of this can be seen also in the adherent basal portion of the peduncle.

CONCLUSIONS.

From a study of the distribution of the bundles in the leaf it is evident that the bundles which supply the spike are not secondarily given off from the main bundles of the petiole, but are themselves the adaxial bundles which can be traced from the base of the petiole into the spike. This would indicate that the spike is not a secondary development upon the leaf, but is a primary portion of it. From a study of the earlier stages of the young sporophyll as well as from the conditions shown in *O. simplex* and certain forms of *O. pendulum* and *O. intermedium*, there seems to be little question that the spike is really a terminal structure, and the writer is inclined to believe that in all cases the spike may be regarded as the apex of the leaf structure and the lamina as lateral with regard to it. If this view be not accepted, it would seem necessary to return to the old view of Mettenius, that the leaf is divided into two equal branches.

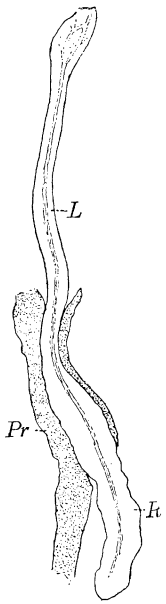

FIG. 16.— Section of the prothallium, *Pr*, and young sporophyte of *Ophioglossum moluccanum*; the latter consists simply of the terminal leaf, *L*, and the primary root, *R*; × 15.

In connection with the question of the terminal position of the sporophyll, the position of the leaf in the embryo may be cited. In *O. moluccanum* — and the same is true in *O. pedunculosum* described fifty years ago by Mettenius,— the young sporophyte (Fig. 16) develops at first only a leaf and root, the definitive sporophyte arising later as an endogenous bud from the primary root. The first leaf must be considered a strictly terminal organ. This embryo corresponds exactly to what might be expected if the hypothesis advanced by the writer — that Ophioglossum probably arose from some form resembling Antho-

ceros — be true. This hypothesis assumes that, by the development of a root from the lower part of the sporophyte and a complete septation of the sporogenous tissue of the sporogonium so that something resembling the spike of an Ophioglossum resulted, there would be formed a plant not very unlike *O. simplex*. We actually have in the embryo sporophyte of *O. moluccanum* a plant which consists simply of leaf and root. Of course the leaf is not sporogenous, but the ancestral form must have developed a sporogenous structure comparable to the spike before the foliage leaf arose. The latter presumably was formed as a lateral outgrowth of the sporogenous portion, as there seems to be some evidence is the case in the young sporophyll of the living species.

THE AFFINITIES OF O. INTERMEDIUM HOOKER.

Ophioglossum (*Ophioderma*) *intermedium* Hook. is apparently a very rare plant. It was originally described by Hooker from

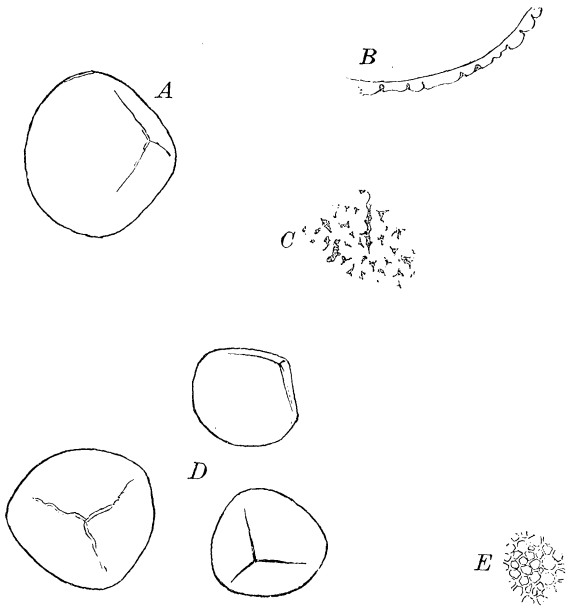

FIG. 17.— *A*, Spore of *Ophioglossum pendulum*, × 500; *B*, optical section of the wall of the spore, more highly magnified; *C*, surface view of the markings of the spore-membrane; *D*, three spores of *O. intermedium*, × 500; *E*, markings of the surface of the spore.

material collected in Sarawak in Borneo. When the writer was in Singapore inquiries were made at the botanical gardens as to the possibility of obtaining material of this species, but it was found that the original locality was lost, and the plant had not apparently been collected since it was first sent to Hooker.

The writer, however, found that this species had been collected near Buitenzorg by Mr. J. J. Smith, of the herbarium of the garden there. He was kind enough to accompany the writer to the place where it had been collected, and it was thus possible to obtain a fair amount of material which was enough to show that the plant is certainly quite distinct from *O. pendulum*, of which it has been supposed (Bitter, loc. cit., p. 469) that it was a mere form, perhaps due to its terrestrial habit. In Buitenzorg it grew in a plantation of bamboo — usually in the accumulation of humus and earth about the roots of the clumps of bamboo. It is a small plant (see Fig. 4) and in its stiff upright habit and much longer peduncle presents a very different appearance from any form of *O. pendulum* — although it is evident that it belongs to the same section of the genus. The plants grew from a small tuberous body apparently developed as a root bud (Fig. 4, B, E) and in this respect as well as in the occurrence of such forms as that shown in Fig. 4, E, where the lamina is almost wanting, it approaches *O. simplex*, with which it may be pretty closely allied. It differs, however, in other respects than that of its habit, from *O. pendulum*. The spores (Fig. 17, D) are decidedly smaller than those of *O. pendulum*, and the delicate reticulate markings of the epispore (Fig. 17, E) are very different from the markings in the latter species.

Stanford University
Jan., 1907